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INFLUENCE OF VARYING OXYGEN TENSION UPON THE RATE OF OXYGEN CONSUMPTION OF FISHES

BY

ANCEL B. KEYS

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The various questions associated with the subject of the respiratory metabolism of animals occupy a central position in modern physiology. The gas exchange has been one of the most fruitful fields of endeavor in recent years, but this productivity has been very largely limited to the air-breathing forms of which man and the common laboratory animals have been studied to the point of what might well be regarded as neglect of other animal life. No doubt such an emphasis is entirely justified on the grounds of expediency, but at the same time it is to be deplored that so little sustained and unexceptionable work has been done on the lower organisms, particularly the poikilotherms. After thirteen years we may still concur with Krogh (1916) that "very few investigations have been undertaken with the definite object of comparing the standard metabolism of different cold-blooded animals."

Since the pioneer investigations of Humboldt and Provençal (1809), a very considerable literature upon the respiration of fishes has grown up, most of it resulting from researches carried out in German and Danish laboratories before the war. Recently two American articles by Powers and Shipe (1928), and by F. G. Hall (1929), have been published on the relation of the rate of oxygen consumption by fishes to the oxygen tension of the (external) respiratory medium. This is a subject that merits attention for a number of reasons: a particularly pertinent one is the fact that all the methods that have previously been used for the determination of the standard metabolism of fishes depend for their validity upon the assumption that the rate of gaseous exchange of the fish is independent of reasonably small changes in the oxygen content of the environmental water. If we accepted the conclusions of the authors cited above, we should have to say that the oxygen consumed by the fish is directly related to the available oxygen of its immediate environment, even when this is within the normal range of oxygen concentrations of natural waters. It is my purpose in the present paper to show that such a conclusion

is entirely unwarranted on the basis of their own data, and furthermore, that if any conclusion can be drawn from *all* the available evidence, a practical independence of the fish's gaseous metabolism to small changes in the oxygen tension of the water is indicated. Before I present the results of my own experiments I shall discuss the experiments of Powers and Shipe and of Hall, and review the literature. Unfortunately these authors seem to be unaware of the existence of the important papers by Henze (1910), Gaarder (1918), and Toryu (1927).

Powers and Shipe used herring, silver salmon, and a viviparous perch, in running sea water in which the pH and the O_2 were determined before and after the passage of the water through the respiratory chamber. Various means were used to vary the oxygen tension and the hydrogen-ion concentration of the incurrent sea water. From one to eight fishes were used together for single periods of only ten minutes and the same fishes were not used in the different experiments. Although the temperature varied from 12.0°C to 20.0°C no correction was made. In figure 1, I have plotted all the data given by them for experiments in which the sea water used was of fairly normal hydrogen-ion concentration (pH 8.2 to 8.4). In addition I have indicated all the rest of their data for pH above 8.00. I have corrected their data to 20.0°C by a correction table worked out from data given in Krogh (1914, 1916), Ege and Krogh (1914), and Ellinger (1915), which has proved satisfactory for approximate corrections in this laboratory. It should be stated, however, that the essential relations are not altered by this correction. Note in the graph that the recorded maximum values are much higher than those previously reported for the oxygen consumption of fishes. The inadequacy of the experimental technique employed is reflected, as might be expected, in results which are so divergent as to be nearly meaningless.

Hall's paper, published in a recent number of the *American Journal of Physiology*, is entitled *The Influence of Varying Oxygen Tensions upon the Rate of Oxygen Consumption in Marine Fishes*. Unfortunately the technique used is undoubtedly faulty in that instead of measuring simply the effect of diminished oxygen tension upon the respiratory metabolism of the fishes, actually the effect measured is that of diminished oxygen tension with a concomitant increased carbon dioxide content, although the author gives no indication of being aware of this fact. Hall used a modified Ege and Krogh apparatus in which the oxygen tension of the water surrounding the fish was controlled by varying the rate of flow; in other words, the oxygen tension was diminished by the respiration of the fish and, as the respiratory chamber was very large, the expired water was mixed

with the surrounding water and was rebreathed by the fish. Of course it is obvious that the fish is giving off carbon dioxide at nearly the same rate as it is using oxygen and the water that is rebreathed is increased in carbon dioxide content to the same degree that it is diminished in oxygen. While the carbon dioxide thus added to the respiratory medium will not exercise its full physiological effect in a

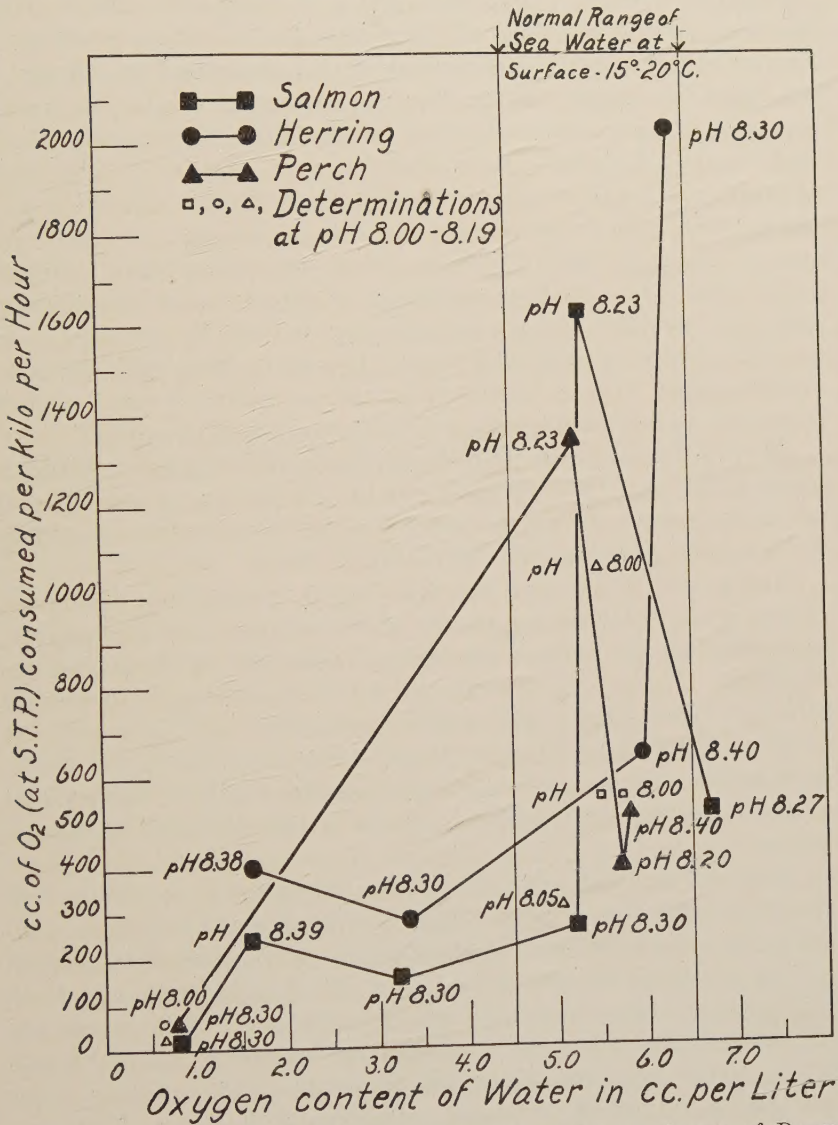


Fig. 1.—Graphical presentation of the results of the experiments of Powers and Shipe, omitting the results for experiments in unusually acid (below pH 8.00) sea water. Values corrected to 20.0° C.

buffered system such as sea water, nevertheless it will lower the pH and will displace the equilibrium of the whole CO_2 -carbonate system, bringing it closer to the point of inflexion on the acid side of the buffer curve. The marked effect of carbon dioxide on respiration has been the subject of a very large number of studies, particularly on the relation of CO_2 to the oxygen-hemoglobin system of the blood (see, for example, Barcroft, 1925, 1928, and L. J. Henderson, 1928). Hall mentions the investigations of Krogh and Leitch (1919) in which it was found that a very small amount of CO_2 diminishes the affinity of fish blood for oxygen, but he does not, apparently, realize the significance of it for his own researches. Wells (1913, 1918) and Shelford and Powers (1915) have shown that fishes are sensitive to very small changes in the pH or carbon dioxide of the water. Wells (1913) showed that fishes are much more sensitive to changes in the CO_2 content of the water than to changes in its dissolved oxygen. Powers (1921, 1922) found that the respiration of marine fishes is profoundly influenced by the hydrogen-ion concentration of the sea water. In his 1922 paper he concludes that "the ability of marine fishes to absorb oxygen at low tension from the sea water is more or less dependent upon the hydrogen ion concentration of the water."

With the foregoing in mind the conclusion to be drawn from Hall's investigation would appear to be that the rate of oxygen consumption is decreased when the oxygen tension of the water is lowered and at the same time its carbon dioxide tension is raised.

The general conclusion that the oxygen consumption diminishes with decrease in the oxygen tension of the medium does not appear to be justified on the basis of the evidence contained in the two papers discussed. There is good evidence that such a direct relationship between oxygen tension and oxygen consumption may hold for some of the marine invertebrates (see Henze, 1910) but it seems that the O_2 consumption of the more active forms may be relatively independent of the available oxygen within certain limits (Vernon, 1896, and Henze).

Winterstein (1908) used an artificial respiration apparatus with the fresh-water fish *Leuciscus* and concluded that the oxygen consumption over a wide range of O_2 tension is independent of the oxygen content of the water, but states "doch ist sie wegen der abnormen Bedingungen, unter denen sich der Fisch befindet, natürlich nur für besondere Zwecke, für kurzdauernde vergleichende Versuche brauchbar." Henze measured the oxygen consumption of two fishes, *Coris* and *Sargus annularis*, in closed containers with water of varying oxygen tension but constant CO_2 content. He concluded that the oxygen consumption is entirely independent of the oxygen of the water down to the threshold of asphyxia.

Gaarder (1918) can be credited with performing some of the most carefully controlled experiments that have been reported on this subject. Although Gaarder's work was not mentioned in either the paper by Powers and Shipe or the paper by Hall, it has been referred to several times in the literature as proving that the oxygen consumption of fishes is in direct proportion to the oxygen tension in the water. For example, Bayliss (ed. 4, 1927 impression, p. 607), states that Gaarder found ". . . in fish, that the consumption of oxygen was, within fairly wide limits, in proportion to its tension." Such a statement gives an entirely misleading picture of Gaarder's results and conclusions. To be sure, Gaarder's data indicate a general trend in the direction of a relationship between the oxygen content of the water and its usage by the fish over a range of oxygen concentration of from one to sixteen cc of O_2 per liter, but the oxygen consumption at oxygen tensions of from 4.5 to 7.5 cc per liter was practically constant, as may be seen from the graph on page 113 of the paper. Moreover, Gaarder himself disclaims any such general interpretation as was made by Bayliss. I quote from the summary given by Gaarder in his article:

Der Sauerstoffverbrauch des Fisches steigt langsam mit einem wachsenden Drucke des im Wasser gelösten Sauerstoffs. Dieses Ansteigen ist aber so schwach, dass bei kleiner Änderungen im Drucke des im Wasser gelösten Sauerstoffs, was unter normalen Verhältnissen im allgemeinen der Fall ist, der Stoffwechsel praktisch als unabhängig von dem Sauerstoffdrucke und konstant betrachtet werden kann.

It should be mentioned that Gaarder used the Ege and Krogh apparatus and kept the fish, *Cyprinus carpio*, under urethane narcosis during the experiments.

Toryu (1927) studied the respiratory exchange in *Carassius auratus* in a stationary system with water of constant CO_2 tension but of different oxygen concentrations. He found that the oxygen consumption is independent of the oxygen tension of the water until its partial pressure is reduced to about a tenth of the normal. He also found that under conditions of beginning asphyxiation the consumption of oxygen is practically nothing, but the production of carbon dioxide goes on with very little diminution until shortly before death.

My own experiments were performed with a different object in view from the investigation of the question under discussion, and water of very low tension was not used. My methods were similar to those employed by Gaarder but I did not narcotize the fishes. Several hundred determinations of the respiratory metabolism were made on the marine killifish, *Fundulus parvipinnis*, at various times of the year. The individual determinations covered periods of from one to

three hours. Oxygen was determined by the Winkler method, using Jacobsen's (1921) technique. The respiratory chambers were so small that it was impossible, with the rates of flow used, for the fish to rebreathe the expired water to any great degree. The temperature was practically constant during any one series of experiments but ranged from 14.6° C to 22.1° C at different times of the year.

Owing to technical difficulties only a few series were performed in which the rate of flow was absolutely constant while the oxygen tension varied, but in none of these experiments was there any indication that small differences in the oxygen concentration of the water has any effect upon the respiratory metabolism of the fish. For example, fish number F₁₁, weight 5.3 grams, consumed 0.14 cc of oxygen per hour per gram in water containing 5.08 cc of oxygen per liter, 0.15 cc in water of 5.22 cc O₂/L., and 0.14 cc in water containing 5.38 cc O₂/L.; these determinations were made at a temperature of 18.1° C and with a rate of flow of 1.00 liters per hour.

In the experiments in which both the oxygen tension of the water and the rate of flow varied, the data similarly point to the conclusion that, within moderate limits, respiration is independent of the available oxygen. In each of these series of experiments all conditions were constant except the available oxygen. It should be emphasized that, although no cannulae were used, the respiratory chambers were so small that practically the entire amount of water flowing through the apparatus was available to the fish for respiration, that is to say, it could pass through the gills.

A rough approximation as to the general order of magnitude of the amount of water pumped through the gills by *Fundulus* such as I used, would indicate that probably a major fraction of the whole amount of water passing through the respiratory chamber also passed through the gills of the fish. At 90 respiratory movements a minute, each of a depth of 0.1 cc, the fish would pump 540 cc per hour (see Winterstein's experiments on *Leuciscus*, 1908). The rate of flow in the experiments presented here was from 660 to 1330 cc per hour on the different occasions. It seems possible, then, that in some cases there may have been a certain amount of "rebreathing" of the respiratory water. A simple calculation will show that with the maximum amount of rebreathing in these experiments, the pH of the inspired sea water could not have been more than one or two hundredths of a pH unit more acid than it was before entering the chamber (see Legendre, 1925, p. 134). In all the experiments where the hydrogen-ion concentration was measured before the water entered the chamber it was practically constant between 8.1 and 8.2 pH.

In the following table I have summarized the results in nine representative series of experiments. The oxygen concentration of the water entering the respiratory chamber is given in the columns headed "O₂ cc/L in water"; the values in the columns "cc O₂ available per hour" were obtained by multiplying the rate of flow by the oxygen concentration and represents the total oxygen available for respiration per hour.

TABLE 1

Fish number	Weight in grams	Temperature C	O ₂ cc/L in water	Rate flow L/hour	cc O ₂ available per hour	cc O ₂ used per hour per gram
M 14	4.7	18.1	5.26	1.01	5.31	0.18
M 14	4.7	18.1	4.90	1.06	5.19	0.18
M 15	3.3	18.2	5.11	1.12	5.72	0.15
M 15	3.3	18.2	5.05	0.92	4.65	0.14
M 16	5.4	17.9	5.13	1.15	5.90	0.16
M 16	5.4	17.9	5.05	1.23	6.22	0.17
M 17	5.5	18.4	4.96	1.13	5.61	0.19
M 17	5.5	18.4	5.04	0.90	4.54	0.20
M 18	2.6	18.6	5.00	1.08	5.40	0.21
M 18	2.6	18.6	5.00	1.21	6.05	0.23
M 48	5.3	20.9	4.95	1.15	5.70	0.12
M 48	5.3	20.9	4.70	1.11	5.22	0.12
M 49	2.5	20.9	4.75	1.11	5.27	0.22
M 49	2.5	20.9	4.74	0.66	3.13	0.23
M 54	6.6	21.3	4.64	1.33	6.17	0.13
M 54	6.6	21.3	4.76	1.33	6.33	0.14
M 55	4.3	21.2	4.56	0.91	4.15	0.21
M 55	4.3	21.2	4.76	1.05	5.00	0.21

NOTE: The values given in the table for the oxygen consumption have all been corrected to a standard temperature of 20.0° C by the correction table mentioned previously. This correction, of course, can have no influence upon the relation of the determination within any single series. Most of the values given for oxygen consumed represent the average of two or more determinations. The experiments tabulated include all those available in which duplicate determinations were made on the same fish at the same temperature but at different levels of oxygen concentration or of rate of flow.

It will be clear from a consideration of all the data and the discussion given above that it is not yet possible to draw any very general conclusions as to the influence of differences in the oxygen content of the respiratory medium upon the rate of oxidative metabolism of fishes. However, it seems equally clear that, in the forms studied, any such influence must be negligible in small deviations of the oxygen content of the water or of the available oxygen in the region of normal oxygen concentrations occurring in nature. It follows that it should

be possible to determine something in the nature of a basal metabolism of fishes which is fairly constant in water not deviating widely from normal saturation.

Theoretical considerations have been discussed by Gaarder and Hall. I quote from the latter's paper:

Two views have been held in regard to the effect that variations in the oxygen supply have upon respiration exchange. The first is that the animal cell itself determines its own respiratory exchange and that the oxidative processes going on within it are independent, within wide limits, of the oxygen supplied. According to the second view, the variations in the oxygen supplied must cause variations in the intensity of oxidations since the velocity of the reaction is held to depend upon the number of molecules able to take part in it. If the number of molecules of oxygen become fewer in number, the rate of oxygen uptake by the cell must decline unless their number is so large that it can be considered practically infinite compared with the number of molecules required to carry on normal respiration.

There can be no doubt that in the branchial respiration of fishes the number of molecules of oxygen available is nothing like infinite compared to the number actually required to carry on the normal oxidative processes. Calculations of the oxygen content of the inspired water and of the expired branchial water (which corresponds to the alveolar air of mammals) show that from one-third to one-tenth of all the oxygen molecules in the inspiratory water are removed or used up during the passage past the gill membranes. If we analyze the situation at the actual surface of the gill membrane as was done by Gaarder, it would seem that a much greater proportion of the oxygen molecules in actual contact with the membrane during their passage are removed from the water. The results of actual oxygen consumption experiments, such as given above, clearly indicate that such a naïve application of mass law principles is inadmissible. It is well known that such a mass law relation does not hold in the mammals (see Barcroft's book in which the extensive literature is reviewed), which possess a sensitive self-regulatory mechanism that compensates all normal variations in the oxygen content of the air so that the metabolic rate remains practically unchanged. I have already called attention to the work of Vernon and Henze upon some of the larger marine invertebrates which appeared to possess a similar ability to extract oxygen at a constant rate independently of its tension in the water. Nomura (1926) reports that the oxygen consumption of *Caudinia* is at every instant proportional to the oxygen tension of the environment. Such divergencies might well be expected in widely differing forms, but in some cases different authors report diametrically opposed results from experiments upon similar animals. For example, Amberson (1928) states that the respiratory exchange of

Paramecium is practically independent of the O_2 concentration of the medium, while Kalmus (1928) reports that the respiration of *Paramecium* is directly proportional to the partial pressure of oxygen in the environment.

The conclusion is forced that no general statements can be made with regard to the effect of the oxygen tension of the environment of aquatic organisms. Some species appear to be uninfluenced by the O_2 tension within fairly wide limits, while others would appear to use oxygen in exact proportion to the oxygen in the medium. Between these extremes there are probably many species whose respiratory exchange is affected by changes in the water but not in proportion to these changes. The fishes so far investigated seem to be practically independent, in their respiration, of the oxygen concentration of the water within a restricted range of this last. Finally, as would be expected, it is safe to say that at or near the asphyxial level of oxygen concentration the oxygen consumption of fishes falls to very low levels.

SUMMARY

The question of aquatic respiration, in spite of its importance in comparative physiology, oceanography, and ecology, has been very inadequately investigated. Two recent papers on the oxygen consumption of fishes and the oxygen tension of the environment purport to show that there is a direct relation between these two, even within the normal range of oxygen tensions of normal waters. It is here shown that this conclusion is unwarranted at present. The literature overlooked by their authors is reviewed and the results of experiments on the Pacific marine killifish, *Fundulus parvipinnis*, are presented. It is believed that at the present time the only conclusions that can be drawn with regard to the effect of the O_2 concentration of the environment upon the respiration of fishes are: (1) the gas exchange of the fish is probably relatively independent of small deviations from the usual oxygen tension of the medium; (2) the respiration of fishes is very markedly decreased at or near the asphyxial level of oxygen tension; and (3) it should be quite possible, by employing modifications of methods previously used, to determine something in the nature of a standard metabolism of fishes.

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